

## BOOK REVIEWS

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### EVERYTHING YOU EVER WANTED TO KNOW ABOUT SPECIATION (BUT WERE AFRAID TO ASK)

**Speciation and its Consequences.**—D. Otte and J. A. Endler, eds. 1989. Sinauer Associates, Inc., Sunderland, Massachusetts. xiii + 679 pp. \$29.95 (paper), \$50.00 (cloth).

Vrijenhoek's contribution for this 25-chapter edited volume, in which he describes the origin of parthenogenetic clones from sexual populations of *Poeciliopsis* fish, reminds us that sex and speciation are intimately related. In *Poeciliopsis*, the genetic diversity of sexual lineages allows them to exploit heterogeneous environments. Triploid clones derived from sexual lineages freeze sexual genotypes, and interdemic selection sorts out these genotypes relative to the environment. Sexual lineages respond to habitat changes and fragmentation by speciating, whereas clonal lineages respond by going extinct. By analogy, if sex is the symptom, speciation is the disease. However, one should not falsely conclude that there is a subject safe from contention in these contributed papers based on a symposium celebrating the 175th anniversary of the founding of the Academy of Natural Sciences of Philadelphia. In this case you need only read Gill's contribution, in which he asks how can it be that 8,000 out of the 30,000 orchid species do not reward their pollinators and set fruit only 1–8% of the time? The editors preface the book by suggesting that it fulfill three purposes: 1) to illustrate the diverse patterns and processes involved in speciation and differentiation; 2) to explore the consequences of this diversity for ecological, paleontological and systematic studies; 3) to present the "extreme diversity of concepts and viewpoints" (p. xii) on speciation. Their success in this endeavor is enhanced by the fact that current questions about speciation are recurring and fundamental questions on the subject. The various means by which biotic diversity multiplies ensures the variety of viewpoints used to explain that diversification.

The most fundamental issue dealt with by many of the contributors entails the nature of species and whether any single definition is optimal. Endler asks if a species is considered a snapshot of present-day organismal interactions, as stressed in reproductive and recognition concepts, how can we avoid a phenetic approach to delimiting species? If we adopt the cladistic species concept do we gain the ability to study speciation patterns at the expense of understanding present-day anagenetic change? Or must we recognize that populations, not species, are the fundamental unit of evolution—as argued by Nelson—and, therefore, species evolve just like genera, families, and other higher taxa? If there is a consensus, it is to the degree that we can delimit the disadvantages of all species definitions so far proposed. Templeton endorses a cohesion concept, whereby the species is "the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (p. 12). Cracraft advocates a cladistic definition, i.e., a species is "an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters,

and within which there is a parental pattern of ancestry and descent" (p. 34). Futuyma and Larson advocate the more theoretical cohesion species concept, yet examine the properties of these species in a cladistic framework. Cracraft illustrates how reliance on reproductive isolation as a criterion for species diagnosis can obfuscate cladistic relationships when hybridization occurs between non-sister species. Larson illustrates the opposite syndrome, i.e., salamanders that don't evolve morphologically, but have become genetically distinct, parapatric entities. Patton and Smith argue that biological species will always be parapatric, because speciation involves isolation and derivation of peripheral populations. This last argument can be made irrelevant by decoupling delimitation of sister species from cladistic analysis. The former focuses on the cohesion of species, whereas the latter attempts to determine the hierarchical patterns of sister-group relationship. Such decoupling is necessary as certainty regarding the attributes of ancestors is not possible.

The diversity of opinions on founder and sympatric speciation is also well represented. Lynch reviews distributional data in light of cladistic relationships and concludes that allopatric speciation accounts for over 70% of the speciation events across a number of vertebrate taxa, whereas peripheral speciation—both "microvicariance" of small peripheral portions of an ancestral range and founder events—account for only 5–10%, and sympatric speciation 5–20%. His analysis admits the possibility of sympatric speciation when the range of one species is entirely contained within the range of its sister, claiming this to be a more parsimonious solution than a vicariant event followed by dispersal. By this interesting argument, vicariance and dispersalist biogeographers become strange bedfellows, sharing the viewpoint that sympatric distributions are due to secondary dispersal. Lest we sense agreement, Barrett advocates founder events and mating system changes in heterostylous plants as one means for diversification, whereas Barton argues that any founder events would leave a trail of reduced heterozygosity, which we do not see.

Recent developments regarding sympatric speciation are well represented, with three chapters presenting recent field data in conjunction with discussions on prior models based on aspects of this mechanism. A fourth chapter by Diehl and Bush offers a new model incorporating habitat preference and assortative mating. All contributions go beyond whether sympatric speciation might occur and how common it might be. The current emphasis focuses on the multiplicity of conditions under which sympatric speciation is the most supportable mechanism. Factors such as habitat association (Tauber and Tauber, Diehl and Bush), infraspecific polymorphism and resource partitioning (Wilson), and frequency and density dependent selection (Grant and Grant) are investigated.

The interaction of species via hybridization, infraspecific reinforcement, and character displacement is also covered. Butlin examines a linear infraspecific hybrid zone in search of reinforcement and does not find it. Harrison and Rand present a more complicated interspecific mosaic hybrid zone which is associated with differences in habitat. Hewitt argues that intrinsic factors as well as differences in habitat may cause coincidence of multiple clines, and the resultant hybrid zone.

Empirical studies can offer new directions for theoretical studies. Otte presents an overview of species patterns and diversity of Hawaiian crickets (there are lots of them). The potential for using these musical creatures for studies of character displacement and reinforcement has yet to be explored. Wake et al. present a detailed

investigation of a narrow hybrid zone in the classical ring species, *Ensatina eschscholtzii*, using morphological and biochemical data. Ryder et al. present chromosomal divergence in African dik-dik antelopes and its implication for managing captive vertebrates.

Community evolution is investigated by ecologists who are now *emphasizing* that historical factors impact present-day community structure. Both Roughgarden and Pacala, and Ricklefs present the taxon cycle as a general—or at least sort of general—model of community organization. The former analysis incorporates paleontological data to provide a historical context. Paleontological presentations are otherwise conspicuously absent, although Nelson's discussion of species is most comprehensible from a paleontological viewpoint. Ricklefs also suggests that comparison of traits of sister groups can elucidate factors affecting their respective diversity, a viewpoint seconded by Larson. Futuyma suggests that speciation is the means by which anagenetic change is preserved, and therefore increased speciation should be correlated with increased anagenesis, all other things being equal.

Whereas the editors were cautious about claiming to assemble a consensus view on speciation, there appears to be a consensus forming with regard to methodology. Speciation is increasingly being viewed in its historical context, and cladistic analysis is the means to present that context. Contention about the nature of species may sort itself out as we more carefully define just what we want to accomplish in any particular analysis. Sympatric speciation studies are clearly becoming more and more sophisticated. A comparison of the data generated by research programs either supporting or denying its existence aptly illustrated who is contributing to science and who isn't.

In summary, this book contains numerous thought provoking contributions that will enhance the understanding of any reader. Far from being an "advances" volume that gets dusty on the shelf, this book ought to be repeatedly consulted. Its use will no doubt stimulate further advances in evolutionary biology and systematics.—*James K. Liebherr, Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999.*

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**Invertebrate-Microbial Interactions: Ingested Fungal Enzymes in Arthropod Biology.**

M. M. Martin. 1987. Cornell University Press, Ithaca and London. 148 pp., illus. \$32.50 hardbound, \$14.95 paperback.

This is the first volume in a series titled *Explorations in Chemical Ecology*, edited by T. Eisner and J. Meinwald. In the preface, author Martin describes how he evolved from organic chemist to chemical ecologist during his 20 year research career. Chapter 1 introduces the reader to the subject by lucidly explaining the chemistry of digestion of cellulose, hemicellulose and pectin. Arthropods that are known or suspected to be capable of digesting these substrates, usually with the aid of microbial enzymes, are reviewed and discussed, with a nod to the pioneering research of P. Buchner, L. Cleveland, R. Hungate and W. Trager.

Chapter 2 brings the reader to the rather complex affairs of the fungus-growing